NOTES ON THE MORPHOLOGY AND NOMENCLATURE OF THREE MEMBERS OF THE EUPLOTIDAE (PROTOZOA: CILIATEA)

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INTRODUCTION

ALTHOUGH members of the genera *Euplotes* Ehrenberg, 1830 and *Aspidisca* Ehrenberg, 1831 are commonly observed in marine and freshwater samples, they are often difficult to identify to the species level. In recent years a considerable effort has been devoted to the species problem in these two genera particularly in the case of the genus *Euplotes*. Tuffrau (1960) introduced the application of the silver-line system or argyrome as a taxonomic feature for the latter genus which made it possible for the first time to determine the identities of some *Euplotes* species and recently these ideas have been extended by Curds (1975). Tuffrau (1964) further applied silver-impregnation methods as a means of identifying species of *Aspidisca* but few have followed his lead.

The revisions of Borror (1972) and Curds (1975) concerning the order Hypotrichida and genus *Euplotes* respectively contain lists of synonyms for species of *Euplotes* and *Aspidisca* with which other authorities do not always agree. In several cases, however, these disagreements are little more than matters of opinion based on sparse and inadequate evidence. Nevertheless these works have provided a stimulus to gather more data about these organisms in an attempt to ascertain their specific identities.

The aim of the present paper is to provide further information on three previously known members of the Euplotidae Ehrenberg, 1838. In particular, the nomenclature of *Aspidisca cicada* (Müller, 1786) Claparède & Lachmann, 1858 is discussed in detail and its silver-line system described for the first time. A new form of *Euplotes aediculatus* Pierson, 1943 is described and *Euplotes daidaleos* Diller & Kounaris, 1966, a species hitherto unknown outside the United States of America, is redescribed.

MATERIALS AND METHODS

SOURCE AND CULTIVATION. Samples of water, associated weed and débris were collected from two different freshwater sources. Samples containing *Aspidisca cicada* and *Euplotes daidaleos* were collected from an artificial pond located in the grounds of the University of Copenhagen, Denmark, in September 1974 and these were airmailed back to London in 5 ml aliquots. Samples of water containing *Euplotes aediculatus* were collected from an indoor cold freshwater aquarium in the

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British Museum (Natural History). In all cases the wild material was placed in Petri dishes of sterile freshwater Erdschreiber solution (Medium 1, Committee on Cultures, Society of Protozoologists, 1958). Several hypotrichous ciliates grew in these cultures which were then isolated, cloned and maintained in the same culture medium. It was found that a thin layer of Musgrave & Clegg's agar (2·5% agar, 0·5% sodium chloride and 0·5% Liebig's beef extract in distilled water) covered with Erdschreiber solution supported the growth of many more organisms than the latter solution alone. This method was therefore routinely adopted when large populations of organisms were required for staining procedures.

STAINING PROCEDURES. Silver-line preparations to display the dorsal and ventral argyrome patterns were made following the 'dry' method of Klein (1958). This method proved to be far more reliable and rapid than the conventional 'wet' method (Corliss, 1953) or the protargol method (Tuffrau, 1967). Nuclei were stained using Dippell & Chao's modification of DeLamater's basic fuchsin as described by Sonneborn (1950). The nuclei of the cells were stained after fixation by air-drying rather than using chemical fixation methods.

RESULTS

Aspidisca cicada (Müller, 1786) Claparède & Lachmann, 1858

NOMENCLATURE. The nomenclature of the organism commonly, but erroneously, referred to as *Aspidisca costata* (Dujardin, 1841) Stein, 1859 is a lengthy series of synonyms, mixed identities and general taxonomic confusion. Since a complete historical account has already been given by Brown (1968) only the major points and recent developments will be mentioned here to support the case made by the latter worker.

Brown (1968) correctly pointed out that Müller (1786) was the first to describe *Trichoda cicada* Müller, 1786, an organism with several longitudinal ribs, and presented figures that are clearly recognizable as the organism under consideration. Bory (1826) later emended the generic name to *Coccudina* Bory, 1826 and specifically refers to Müller's (1786) descriptions in his own description of *Coccudina cicada* (Müller) Bory.

In 1831, Ehrenberg erected the genus *Aspidisca* Ehrenberg, 1831 and later the same author described an organism with crenated or toothed longitudinal ribs which he called *Oxytricha cicada* Ehrenberg, 1838. Dujardin (1841) also described an organism with five or six tuberculated dorsal ribs which he recognized as being identical to *O. cicada* Ehrenberg, but considered that it should be included in the genus *Coccudina*. Clearly Dujardin (1841) could not simply emend the generic name of the species since the specific name was already preoccupied by *C. cicada* (Müller), a species with smooth longitudinal dorsal ribs. Dujardin (1841) therefore named his species *Coccudina costata* Dujardin, 1841, having *O. cicada* Ehrenberg as a synonym. Thus at this point in time there were thought to be two distinct organisms, one with smooth ribs – *C. cicada* (Müller) and one with crenated ribs – *C. costata* Dujardin.

In 1858 Claparède & Lachmann transferred several species of the genera *Coccudina* and *Oxytricha* to Ehrenberg's genus *Aspidisca*. Among the species they transferred was *Aspidisca cicada* (Müller, 1786) Claparède & Lachmann, 1858, an organism with smooth dorsal ribs and furthermore concluded that 'it is not impossible that *A. cicada* (Müller) is identical to *O. cicada* Ehrenberg'. Claparède & Lachmann (1858) also briefly mentioned *C. costata* Dujardin and said that in their opinion it was probably a member of the genus *Aspidisca*. The confusion really began with Stein (1859) who was the first to use the combination *Aspidisca costata* (Dujardin) which he considered to be identical to *C. costata* Dujardin even though the figures of this author (Stein, 1859) did not indicate the presence of teeth nor tubercles along the dorsal ridges. Nevertheless, he did not regard this species to be identical to *O. cicada* Ehrenberg. Since that time, authorities such as Kent (1880–1882) and Kahl (1932) have referred to Stein's (1859) description so that organisms with smooth dorsal ribs have been called *Aspidisca costata* (Dujardin) Stein instead of *Aspidisca cicada* (Müller) Claparède & Lachmann. The name *A. costata* should correctly only be used in connection with an organism with crenated or tuberculated dorsal ribs as was originally intended by Ehrenberg (1830) and Dujardin (1841).

Although Brown (1968) indicated most of these points in great detail, Borror (1972) listed *Aspidisca costata* (Dujardin) as a major synonym and considered *Aspidisca cicada* (Müller) to be a minor synonym of *Aspidisca lynceus* (Müller, 1773) Ehrenberg, 1831 in his review of the hypotrichs. More recently Diller (1975) agreed with the conclusion of Borror (1972) on the grounds that Müller (1786): 'Had assigned it to a different genus, *Trichoda*'. However, following the International Code of Zoological Nomenclature (Stoll *et al.*, 1964), Article 23 concerning the Law of Priority states: 'The valid name of a taxon is the oldest available name applied to it provided that the name is not invalidated by any provision of this code'. In this particular case, *Aspidisca cicada* (Müller) is the oldest available name for the taxon. Since the generic name *Aspidisca* Ehrenberg did not exist in 1786, Diller's (1975) comments are inappropriate.

It is suggested therefore that the evidence of Brown (1968) be accepted and the organisms often erroneously referred to as *Aspidisca costata* (Dujardin) Stein be correctly referred to as *Aspidisca cicada* (Müller) Claparède & Lachmann. A list of synonyms is given below:

Aspidisca cicada (Müller, 1786) Claparède & Lachmann, 1858: syn. *Trichoda cicada* Müller, 1786: *Coccudina cicada* Bory, 1826: *Coccudina costata* Dujardin, 1841: *Coccudina cicada* Dujardin, 1841: *Aspidisca costata* Stein, 1859: *Aspidiscopsis bengalensis* Ghosh, 1921: *Aspidisca sulcata* Kahl, 1932: *Aspidisca costata* f. *tetracirrata* Tucolesco, 1962.

The original drawings of these organisms are often poor by modern standards and it would appear highly likely, particularly from Dujardin's (1841) figures, that *A. costata* (Dujardin) is a junior synonym of *A. cicada* as is shown above, whereas Borror (1972) attributed *C. cicada* Bory an organism with dorsal ridges as a junior synonym of *A. lynceus* an organism without dorsal ridges.

In spite of the historical taxonomic problems of *Aspidisca cicada* this organism is usually simple to identify since there are few freshwater species of the genus and

A. cicada is the only one with six prominent longitudinal dorsal ridges. The number of dorsal ridges in this species does vary, for example, Diller (1975) reported that although his specimens usually had 6–7 ridges the number actually ranged from 3 to 10. From this information it seems likely that *Aspidisca sulcata* Kahl, 1932 is a synonym of *A. cicada* since the difference lies only in the number of dorsal ridges.

Description. When one considers the genus as a whole the problems of identification and synonymy become acute. Such a situation is also found in the closely related genus *Euplotes* where the problem has been greatly alleviated, but not solved, by the application of silver-impregnation methods (Tuffrau, 1960 ; Curds, 1975). The silver-line system or argyrome of some species of *Aspidisca* has been published (Tuffrau, 1964). *A. cicada* has been the subject of several morphological papers (Hamm, 1964 ; Brown, 1966 ; Diller, 1975) but none of these has included a description of the dorsal and ventral argyrome, even though Diller (1975) employed silver-impregnation methods in his study. In *Euplotes* (Tuffrau, 1960 ; Curds, 1975), the dorsal silver-line system has been of considerable value in identification and although the detail of the argyrome, such as numbers of kineties, is not as stable as was orginally hoped (Génermont *et al.*, 1976) the gross geometry has yet to be shown to vary within species of that genus. It is hoped that the gross patterns of the dorsal

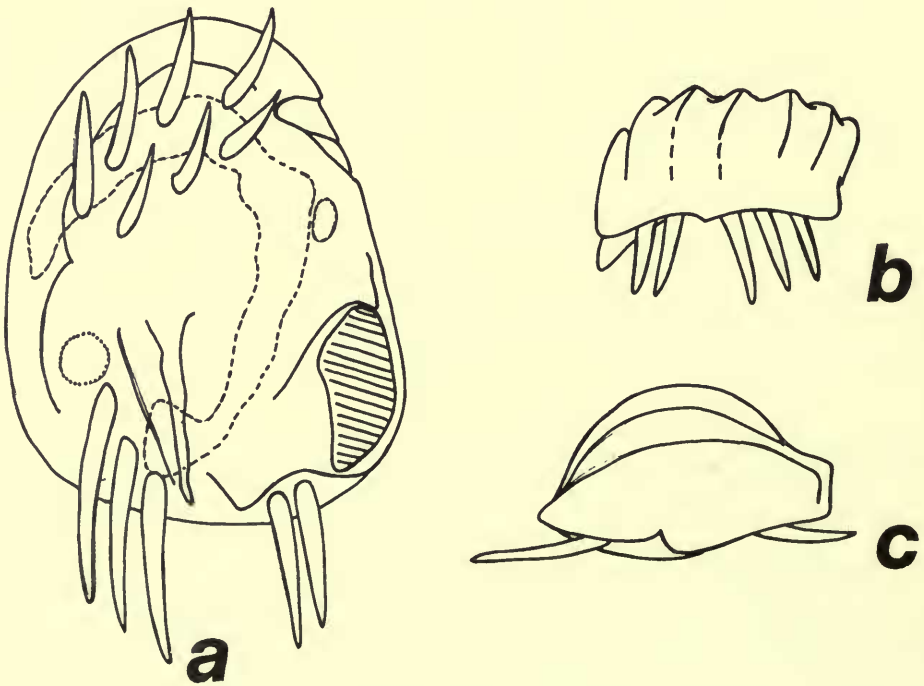

Fig. 1. External morphology and nuclear features of *Aspidisca cicada*. (a) ventral surface showing cirri, adoral zone and nuclei ; (b) posterior aspect showing dorsal ridges ; (c) lateral aspect.

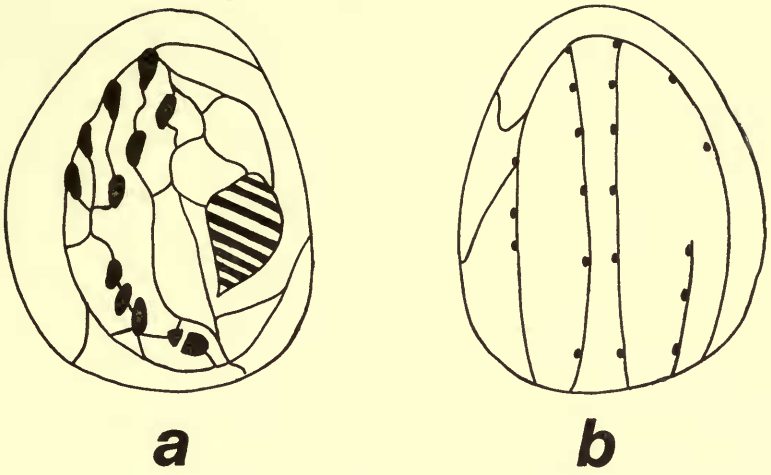

FIG. 2. Silver-line system of *Aspidisca cicada*. (a) ventral argyrome ; (b) dorsal argyrome.

silver-line system of *Aspidisca* will prove to be of similar diagnostic value. In any event an extra character is always to be welcomed for identification purposes.

The external morphology of *A. cicada* has been described on several occasions and the descriptions by Hamm (1964), Brown (1966) and Diller (1975) are the most comprehensive. Their accounts differ little from each other and the specimens examined in the present study conform with their descriptions unless stated otherwise. The diagrams of the external morphology and nuclear structure (Fig. 1) are given so that the descriptions of the argyrome can be linked to other details of the animal for future reference.

The dorsal and ventral silver-line systems of *Aspidisca cicada* are shown in Fig. 2 and are very similar to those illustrated by Klein (1929) and von Gelei (1939) for *Aspidisca lynceus*. However, a comparison between these two species shows that *A. lynceus* has more kineties and more dorsal bristles than *A. cicada*. The ventral argyrome and the positions of the seven frontoventral cirri, the five transverse cirri and the adoral zone of membranelles are easily seen (Fig. 2a). Although hundreds of specimens were stained and examined, the anterior ventral ciliary structure referred to by various names in the literature was never displayed by the dry silver method used, but it could easily be seen beating in the anterior notch in living specimens. Neither Klein (1929) nor Diller (1975) seemed to have had difficulties staining this ciliary structure even though Klein used the same silver-impregnation method.

The dorsal argyrome of *A. cicada* (Fig. 2b) is a simple structure by comparison with those in species of the genus *Euplotes* and is composed of a total of five dorsolateral kineties. There are two outer kineties that encircle the perimeter of the animal to join anteriorly, two kineties that travel longitudinally either side of the longitudinal axis of the body and a single short kinety on the right that occurs only in the posterior third of the body. Silver impregnation clearly displays the positions of the dorsal cilia or bristles and numbers of these were found to be constant in the clone

examined. There were 3, 6, 6, 3 and 2 bristles respectively in the kineties from left to right. Brown (1966) stated that *A. cicada* had no dorsal bristles and indeed they are extremely difficult to see in living specimens. Diller (1975) also disagreed with Brown (1966) on this point and stated that he had seen indications of dorsal bristles similar to those found in *Euplotes*. Other workers (Tuffrau, 1964; Deroux & Tuffrau, 1965) have shown the presence of dorsal cilia in other species of *Aspidisca*.

Slides showing silver-line systems and nuclei have been deposited in the slide collection of the BM(NH), reg. nos 1975:7:4:5–7.

Euplotes aediculatus Pierson, 1943

Euplotes aediculatus Pierson, 1943 has been the subject of several papers on *Euplotes* taxonomy (Pierson, 1943; Tuffrau, 1960; Pierson *et al.*, 1968; Carter, 1972) and a complete account of the confusion and misidentifications recorded in the literature concerning this species has already been given by Curds (1975).

At least four species of *Euplotes* have been described that have varieties with wing-like extensions to their lateral margins or extensions to their dorsal ridges. Kahl (1932) stated that *Euplotes patella* (Müller, 1773) Ehrenberg, 1838 has five varieties and based four of these on the size and location of the dorsal ridges. Similarly Kahl (1932) listed three varieties of *Euplotes muscicola* Kahl, 1932 on the basis of dorsolateral ridging. Two species, *Euplotes carinatus* Stokes, 1885 and *Euplotes novemcarinata* Wang, 1930, have been described as species mainly on the basis of possessing large dorsolateral ridges. Kahl (1932) and subsequent workers (Borror, 1972; Curds, 1975) have tended to consider *E. carinatus* to be a synonym for *E. patella*, but *E. novemcarinata* is still regarded as being a possibly valid species. Other hypotrichs such as *Aspidisca cicada* have also been noted to have several different heights in their dorsal ridges (Hamm, 1964).

An organism collected from an indoor unheated freshwater aquarium was noted to possess large wing-like processes on the dorsal surface and left lateral border. On the basis of these structures and general morphology the organism was suspected to be a variety of *Euplotes patella*. An individual with ridge extensions was isolated and the initial descriptions given here refer to that clonal culture.

The external morphology and nuclear structure of the organism mentioned above is illustrated in Fig. 3. Two of the six dorsal ridges were extended, the central ridge was large and there was a slightly smaller one on its right. In addition, the left border of the animal projected out and curved ventrally (Fig. 3b, c). On the ventral surface (Fig. 3a) there were nine frontoventral, five transverse and four caudal cirri. The nuclear features were the first indication that this species was a variety of *Euplotes aediculatus* rather than *E. patella*. The macronucleus of both species is C-shaped but in the case of *E. aediculatus* there is much more of a distinct flattening of the anterior portion.

Silver-line preparations (Fig. 4) showed that the organism was indeed *Euplotes aediculatus* since the dorsal argyrome was of the double-eurystomus type (Curds, 1975) rather than the double-patella type. There were eight dorsolateral kineties (Fig. 4), but the collapse of the extended central ridge, during air-drying, made it

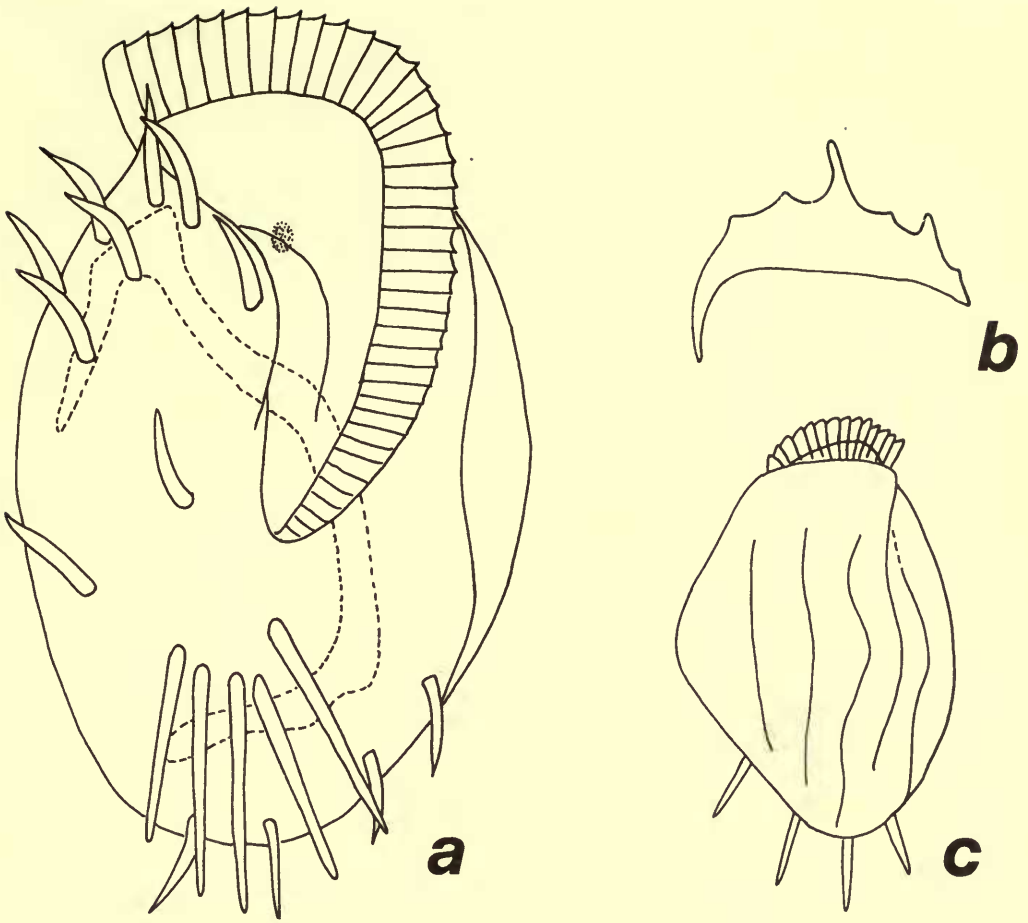

FIG. 3. External morphology and nuclear features of *Euplotes aediculatus*. (a) ventral aspect showing cirri and nuclei; (b) transverse section through centre to show extended ridges and lateral border; (c) dorsal aspect showing extended lateral border.

difficult to count accurately the numbers of cilia in the central kineties – however they were estimated to be about 25. On the basis of the nuclear and argyrome features this species was identified to be *E. aediculatus*. This appears to be the first record of *E. aediculatus* having extensions to the ridges and furthermore it is the first time that a variety such as this has been traced to its parent species by the use of its silver-line system.

After a few months, examination of the clonal culture showed that some of the cells had lost their ridge and lateral extensions. Unfortunately, soon after this observation the clonal culture was lost due to a malfunction of the cooled incubator in which it was kept. Samples taken from the same aquarium showed the presence of a *Euplotes* species of the same size and general appearance but without projections

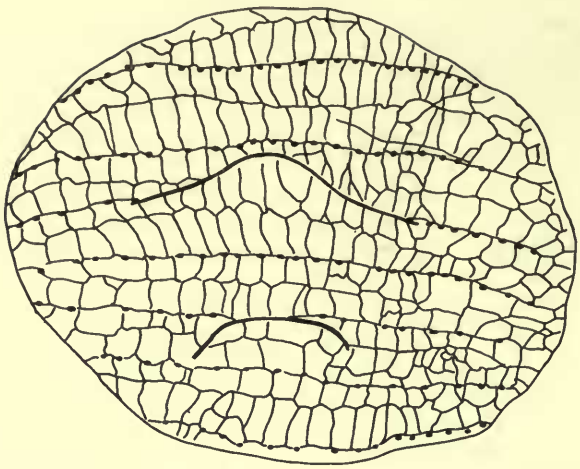

FIG. 4. Dorsal argyrome of *Euplotes aediculatus* specimen with extended dorsal ridges.

and large ridges. Silver impregnation and nuclear stains of these organisms showed that this was a 'normal' *Euplotes aediculatus* with a dorsal argyrome similar to that shown in Fig. 4. Although it is possible that the first organism had been replaced by a second it seems unlikely and in view of the observations on the original clone it would appear that the 'abnormal' form had reverted to the 'normal' shape. Why 'abnormal' forms like this should be produced remains a mystery. There seems little advantage in possessing large ridges and lateral borders and to the author's knowledge no theories have yet been published in the literature concerning this phenomenon.

Slides of both 'normal' and 'abnormal' forms of *Euplotes aediculatus* showing the silver-line systems and nuclear features have been deposited in the slide collection of the BM(NH), reg. nos 1975:7:4:3–4 ('abnormal') and 1975:11:19:1–2 ('normal').

Euplotes daidaleos Diller & Kounaris, 1966

Diller & Kounaris (1966) described the species *Euplotes daidaleos* which they obtained from an artificial pond in Philadelphia, U.S.A. This organism contains symbiotic zoochlorellae and appears to be the only record of a species of *Euplotes* containing a green symbiont that has been identified using modern methods. There are many other records of zoochlorellae-bearing *Euplotes* in the literature (Curds, 1975) but in all other cases these identifications are open to considerable doubt since the host cells were not stained with silver.

The organism described in the present paper was isolated from an artificial pond situated in the grounds of the University of Copenhagen, Denmark. On arrival in our laboratory the organisms were maintained in a dark cooled incubator at 18 °C. On the basis of its size and general shape it was provisionally thought to be *Euplotes patella*. However, after staining the nucleus and silver-line system it soon became apparent that this provisional identification was incorrect. The results of these

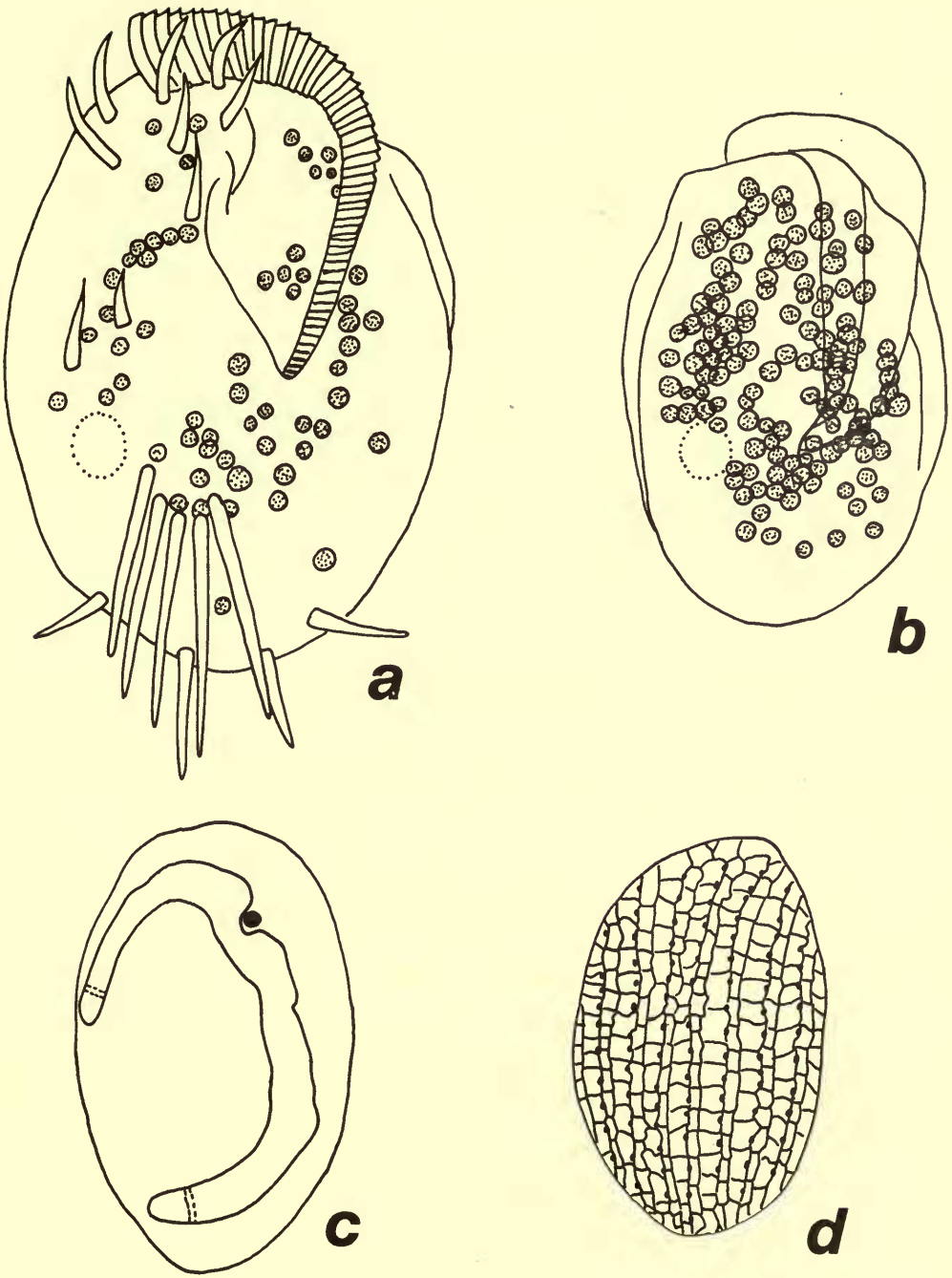

FIG. 5. *Euplotes daidaleos*. (a) cell cultivated in dark ; (b) cell cultivated in light ; (c) nuclei ; (d) dorsal argyrome.

staining techniques are shown in Figs 5c and d. The dorsal argyrome was of the double-patella type with nine dorsolateral kineties containing 15–17 cilia in the mid-dorsal rows. The macronucleus was found to be an open C-shape with the micronucleus deeply embedded in a depression of the macronucleus. The ventral aspect of the animal is shown in Fig. 5a which illustrates the positions of the nine fronto-ventral, five transverse and four caudal cirri. Fig. 5a also shows the large numbers of membranelles (about 60 in silver-line preparations) in the adoral zone. From this information the organism was tentatively identified as *E. daidaleos* even though zoochlorellae were not apparent. Closer examination of the cytoplasm revealed the presence of some yellow to light green inclusions although they were too few in number to impart any coloration to the animal as a whole. Some of the cultures were then exposed to light which led to an immediate increase in the numbers of these cytoplasmic bodies and to the depth of colour. Within a week of constant exposure to light the zoochlorellae reached sufficiently high numbers in the cytoplasm to impart a bright green colour to the host cells. Figs 5a and b illustrate the numbers of zoochlorellae in this species of *Euplotes* when cultured in the dark and light respectively. The presence or absence of light did not have any obvious effects upon the rate of growth, nor the peak population, of *Euplotes* supported in the cultures.

On the basis of the dorsal argyrome (Fig. 5d), numbers of membranelles in the adoral zone, nuclear features and presence of symbionts this organism was identified as *Euplotes daidaleos*. This is the first record outside America. The only difference that could be visually detected between the Danish and American strains was the precise shape of the macronucleus. In the case of the American strain (Diller & Kounaris, 1966) the macronucleus was rather more angular than that described here (Fig. 5c). The fact that an organism such as this can be easily recognized from silver-impregnation preparations is encouraging particularly when the sources of material are so remote from each other both in terms of geography and time.

Slides of the Danish strain of *Euplotes daidaleos* showing silver-line systems and nuclear features have been deposited in the slide collection of the BM(NH), reg. nos 1975:7:4:1–2.

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